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Migratory Atlantic salmon as vectors for the transfer of energy and nutrients between freshwater and marine environments

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SUMMARY

1. Annual energy, carbon, nitrogen and phosphorus fluxes across the river mouth by Atlantic salmon were estimated for 18 years (1976–94) in the Norwegian River Imsa. The total energy content of the emigrating smolts in each year varied considerably with a mean value of 237 × 10^3 kJ. That of returning adults also varied between years with a mean value of 141 × 10^4 kJ. One-sea-winter salmon (grilse) made up 65% of the total energy content of the spawners in the river. Dead carcasses remaining in the river after spawning were estimated to have a mean annual energy content of 175 × 10^3 kJ.

2. The net annual energy flux from the sea to the river varied between 48 × 10^3 kJ (1987) and 152 × 10^4 kJ (1989) with a mean of 616 × 10^3 kJ, and a coefficient of variation of 67%. Average net marine import of the returning adults was 83 × 10^4 kJ year^{-1} with a coefficient of variation of 52%. Mean annual export of C, N and P to sea by the smolts was 595, 131 and 22 kg, and by kelts 1535, 352 and 70 kg, respectively, whereas gross import via the adults was 3176 kg C, 735 kg N and 132 kg P. The annual flux across the river mouth was 1046 kg C, 253 kg N and 39 kg P. The net marine import were 1585 kg C, 371 kg N and 60 kg P. The net flux was estimated at 0.2% for nitrogen and 5% for phosphorus of the total river load.

3. The energy flux caused by Atlantic salmon spawning in the River Imsa was relatively high because the general nutrient load in the river is low. Thus, even though most Atlantic salmon survive spawning, their contribution to the nutrient flux in the river is significant.

Keywords: carbon, Imsa, marine import, net energy flux, nitrogen, phosphorus

Introduction

Anadromous species are vectors transporting energy and nutrients from the marine to freshwater environments (Michael, 1998; Minakawa & Gara, 1999) as well as adjacent terrestrial areas (Helfield & Naiman, 2001). The carcasses are important nutrient sources for riparian plants (Bilby, Fransen & Bisson, 1996; Ben-David, Hanley & Snell, 1998), invertebrates (Wipfli, Hudson & Caouette, 1998; Wipfli *et al.*, 1999), and are even consumed by some fish species such as the coastrange sculpin *Cottus aleuticus* in Alaska (Kline *et al.*, 1993).

Together with the eggs, the carcasses of anadromous species provide important resources during a period when other food items are often scarce (Bilby *et al.*, 1998). Carcass mass initially undergo a high rate of mass loss that tapers off with time. The spatial distribution of the marine-derived nutrients is apparently determined by flooding and the activity of piscivorous predators (Ben-David *et al.*, 1998), and Chironomid and Plecoptera larvae are likely to be very important in mediating nutrients and energy transfer between salmon carcasses and other components of

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the freshwater-riparian food web, as found in south-eastern Alaskan streams serving as spawning habitats for pink salmon (*Oncorhynchus gorbuscha*) (Chaloner, Wipfli & Caouette, 2002).

Several studies have demonstrated the importance of Pacific salmon *Oncorhynchus* spp. in the recycling of elements between marine and freshwater habitats in North America (Kline *et al*., 1990, 1993; Bilby *et al*., 1996; Kline, Goering & Piorkowski, 1997; Cederholm *et al*., 1999; Gresh, Lichatowich & Schoonmakes, 2000). Atlantic clupeids *Alosa* spp. (Garman & Macko, 1998) and salmonids *Salmo* spp. have also been viewed in a similar context (Elliott, Lyle & Campbell, 1997; Lyle & Elliott, 1998), but their general importance is uncertain. For both *Salmo* and *Alosa*, the nutrient input has been estimated, and the works emphasis the importance of the elements provided for the structure and dynamics of riparian ecosystems.

In contrast to Pacific salmonids, Atlantic salmonids are iteroparous. Thus, many return to the ocean after spawning instead of dying in the river. This was not included in the first account of the salmonid contribution to the nutrient flux across a river mouth (Elliott *et al*., 1997). This preliminary evaluation was corrected and expanded by Lyle & Elliott (1998) who set the return of postspawners at 25%, based on preliminary results from radio tagging experiments and the survival found in another British river by Mills (1986). Their population estimates were also rough, chiefly based on catch records from anglers, setting rod exploitation rates at either 10 or 30%. These were the probable limits based on the best information available, and for north-east English rivers they estimated a two and eight times higher nutrient import than export in the form of anadromous salmon and trout. The amount of energy transported into and lost within fresh waters by salmonids was not estimated.

Precise estimates of nutrient transport to fresh waters by anadromous fishes can be obtained if all emigrating and immigrating fish are counted and weighed. There are few such 'index rivers' in Europe where the loss of spawning Atlantic salmon in the river is quantified, but one is the Norwegian River Imsa, where salmonid migration has been monitored since 2 May 1975 (Jonsson, Jonsson & Hansen, 1991a, 1998a). The investigations in the River Imsa indicate much higher survival rates of postspawners (kelts) than suggested by Lyle & Elliott (1998) from English rivers. The annual population estimates in the River Imsa allow for estimation of annual variation in the import of nutrients and energy. In this river, fishing is prohibited, and we are not aware of any vertebrate predator catching salmon in the river. There is no information about possible loss of fish to potential scavenges in the river.

We estimated the fluxes of energy, carbon, nitrogen and phosphorus brought into the River Imsa by Atlantic salmon *Salmo salar* L. between 1976 and 1994. Energy and nutrients were estimated for smolts, spawners, kelts and dead fish. Since the adult return to the ocean is higher than that suggested by Lyle & Elliott (1998), but few return to spawn a second time, we hypothesized that the nutrient flux into the river is lower than estimated by Elliott *et al*. (1997) and Lyle & Elliott (1998). By estimating the fluxes of energy and nutrients from the sea to the river, we obtained an account of the energy loss of the population during reproduction, and the magnitude of the nutrients imported to the river. For phosphorous and nitrogen, this was compared with the total export of these elements by the river to the estuary.

Methods

Energy content, organic carbon (C), nitrogen (N) and phosphorus (P) exchange between the River Imsa and the sea by the Atlantic salmon were considered for smolts (downstream migrating juveniles), upstream migrating spawners, kelts (spent fish migrating to sea after spawning) and dead spawners. Mean values were assessed for the River Imsa, south-western Norway (58°50′N, 6°E) over a 19-year period (1976–94). The fish trap in the river, however, was closed in 1980. The smolts, spawners and kelts were sampled in traps, situated 100 m above the estuary of the river, when they were descending and ascending the river. The traps, which have been monitored daily since 1975, catch all ascending and descending fish larger than about 10 cm long. All fish passing the traps were counted, natural tip lengths (0.1 cm; Ricker, 1979) and wet masses measured (0.01 g) and untagged fish tagged with individually numbered Carlin tags (Carlin, 1955). The river, traps and sampling procedures are described in more detailed in Jonsson, Jonsson & Ruud-Hansen (1988) and Jonsson, Jonsson & Hansen (1990, 1998a,b).

The River Imsa supports a small population of anadromous Atlantic salmon (< 200 spawners). The fish smolt as 1 (mean for the period: 14%), 2 (78%) or ≥ 3 (8%) years of age. Most of the anadromous salmon attain maturity as one-sea-winter fish (82%; mean length 61.3 ± 5.9 cm), the rest as two-sea-winter fish (82.4 ± 7.7 cm; Jonsson *et al.*, 1991b, 1998a,b).

Somatic and gonadal energy contents of various life history stages of Atlantic salmon in the River Imsa were studied by Jonsson & Jonsson (2002), and the numbers and biomasses of emigrating smolts and kelts and immigrating adults are from Jonsson *et al.* (1998a,b). The carbon, nitrogen and phosphorus content of the fish were estimated according to Talbot, Preston & East (1986) and Lyle & Elliott (1998).

The flux by Atlantic salmon across the river mouth was due to emigrating smolts and kelts and immigrating adults to the River Imsa each year, the results being a net import to the river [immigrating spawners – emigrating (smolt + kelts)]. Marine derived biomass imported back across the river mouth was due to returning adults, less the original smolt weight of these fish and that of those leaving as kelts.

Results

Energy

The total energy content of emigrating smolts each year varied from 57×10^4 kJ (in 1976) to 374 kJ (1994) with a mean of 237×10^3 kJ (Table 1) and a coefficient of variation (CV) of 61.5%. That of the returning adults was approximately six times higher, varying from 230×10^3 kJ (1987) to 270×10^4 kJ (1989) with a mean of 141×10^4 kJ (CV 50.3%). One-sea-winter salmon (grilse) made up 65% (916×10^3 kJ) of the total energy content of the spawners in the river. The energy content of sexual products (eggs and milt) left in the river varied between 17×10^3 kJ (1987) and 444×10^3 kJ (1989) with a mean of 255×10^3 kJ (CV 49.7%), whereas that of the dead carcasses remaining in the river varied between 38×10^3 and 353×10^3 kJ with 175×10^3 kJ as the annual mean (CV 54.8%). The energy content of the immigrating adults and that of the dead carcasses remaining in the rivers each year was positively correlated, with no indication of a density dependent effect ($r^2 = 0.91$, $P < 0.001$).

Table 1 Energy contents of descending smolts, ascending anadromous adults, gonadal products spawned in the river, dead spawners left in the stream, spent anadromous adults returning to sea and net energy flux in the system [(ascending adults – (descending smolts + kelts)], and marine import [ascending adults-(their energy as descending smolts + kelts)] of Atlantic salmon for the years 1976–94. The fish trap was closed in 1980

Year	Smolts	Ascending spawners	Sexual products	Dead in river	Descending kelts	Net energy Flux	Marine import
1976	570 953	2 145 822	394 538	255 567	1 270 181	304 688	844 587
1977	363 683	2 256 271	406 058	261 591	876 469	1 016 119	1 353 111
1978	275 500	1 976 640	369 326	283 553	816 141	884 999	1 127 446
1979	259 396	1 235 950	222 200	198 926	635 429	341 125	575 822
1981	499 622	1 693 806	405 094	139 286	593 461	600 723	1 085 816
1982	122 038	2 183 255	249 183	323 713	759 387	1 301 830	1 390 452
1983	293 461	928 809	152 897	104 556	295 732	339 616	625 595
1984	198 452	1 085 726	225 959	118 736	405 880	481 394	660 992
1985	149 500	831 600	159 899	101 568	323 941	358 159	491 291
1986	61 776	840 185	182 127	83 807	307 576	470 833	522 297
1987	100 697	230 400	16 613	38 673	82 001	47 702	144 153
1988	294 306	1 125 808	284 231	106 692	464 326	367 176	640 235
1989	185 366	2 708 599	444 387	353 494	1 002 334	1 520 899	1 663 298
1990	251 301	2 408 886	434 528	293 720	857 898	1 299 687	1 520 996
1991	306 814	1 074 570	174 328	134 975	396 154	371 602	660 703
1992	243 572	1 369 796	215 524	175 895	507 497	618 727	824 868
1993	90 880	739 699	133 954	98 003	279 391	369 428	441 754
1994	374	633 690	116 652	82 601	248 268	385 048	371 433
Annual mean	237 094	1 414 973	254 861	175 298	562 337	615 542	830 269
± SD	± 145 879	± 711 477	± 126 551	± 96 053	± 312 219	± 413 209	± 430 745

Mean annual energy content of the kelts returning to sea after spawning was 562×10^3 kJ (CV 55.5%), this being approximately 40% of the energy content of the immigrating adults. The net annual energy flux was the energy of adult Atlantic salmon remaining in the river (ascending spawners – descending (smolts + kelts)), and was between 48×10^3 kJ (1987) and 152×10^4 kJ (1989) with a mean value of 616×10^3 kJ (CV 67.1%). The estimated mean is 2.6 times the energetic content of the smolts, but 2.3 times less than (or 44% of) that of all immigrating adults.

The annual marine energy import of the adults spawning in the river [immigrating adults – (these as smolts + emigrating kelts)] was between 144×10^3 kJ (1987) and 166×10^4 kJ (1989) with an estimated mean at 83×10^4 kJ (CV 51.9%). The estimated mean value is 1.35 times higher than that of the energetic flux since it only includes the energy of salmon surviving to adulthood, and not that of the emigrating fish that died in the sea.

Nutrients

The mean annual river derived export of C, N and P to the sea by smolts was 595, 131 and 22 kg, respectively (Table 2). We do not give values for individual years since the nutrient content accords closely with the energetic content of the fish. The annual gross import of C, N and P via the adults returning from the sea was high with mean values of 3176 kg, 735 kg and 132 kg, respectively (Table 2). The gross import of C, N and P to fresh water by one-sea-winter salmon (grilse) varied highly among years, ranging from 18% in 1983 to 100% in 1985 and 1987. Mean values were 387 kg C, 89 kg N and 18 kg P, respectively. The two-sea-winter fish added just over 30% to these values for one-sea-winter fish. The annual import of these flux materials to the sea by kelts were 1535 kg C, 352 kg N and 70 kg P. As the one-sea-winter fish dominated in C, N and P among the spawners, they also made up the largest part of the kelts and the dead spawners left in the river (76%).

The flux of C, N and P by Atlantic salmon across the river mouth was due to smolts and kelts leaving the river and adults returning to the river for spawning; the results being a net annual import to the river of 1046 kg C. The variation in net import among years was high and ranged between 2706 kg organic carbon in 1989 to 39 kg in 1987. The corresponding value of nitrogen was 253 kg with the total range of variability between 639 and 13 kg, and of phosphorous was 39 kg with the total range of variability between 103 and 2 kg (Table 2). Marine derived import back across the river mouth was due to the returning adults, less their original smolt mass and that of those emigrating as kelts. The net marine import of carbon, nitrogen and phosphorus was 1585 kg, 371 kg and 60 kg, respectively. The range of variability in carbon was between 3060 and 285 kg, of nitrogen 716 and 67 kg and of phosphorus 116 and 11 kg.

Table 2 Mean carbon, nitrogen and phosphorus fluxes ± SD by different life history stages and sea-age groups of Atlantic salmon across the river mouth between 1976 and 1994

	Carbon (kg)			Nitrogen (kg)			Phosphorus (kg)		
	Mean ± SD	Max	Min	Mean	Max	Min	Mean	Max	Min
Smolts	595 ± 366	1432	935	131 ± 80	314	0.21	22 ± 14	54	0.04
Spawners total	3176 ± 1598	6059	537	735 ± 370	1403	124	132 ± 67	252	22
One-sea-winter	2180 ± 1312	5351	329	504 ± 304	1239	76	91 ± 55	223	14
Two-sea-winter	996 ± 850	2909	0	231 ± 197	673	0	42 ± 35	121	0
Spent fish total	1535 ± 761	2884	241	352 ± 174	661	55	70 ± 35	132	11
One-sea-winter	1028 ± 615	2546	149	236 ± 141	583	34	47 ± 28	117	7
Two-sea-winter	507 ± 430	1469	0	116 ± 99	337	0	23 ± 20	67	0
Dead spawners total	511 ± 282	1033	115	117 ± 65	237	26	23 ± 13	47	5
One-sea-winter	387 ± 243	918	68	89 ± 56	210	15	18 ± 11	42	3
Two-sea-winter	125 ± 114	385	0	29 ± 26	88	0	6 ± 5	18	0
Net flux	1046 ± 767	2706	39	253 ± 179	639	13	39 ± 29	103	2
Marine import	1585 ± 813	3060	285	371 ± 190	716	67	60 ± 31	116	11

Discussion

Through their migratory behaviour, Atlantic salmon move energy in the form of organic matter from the sea to fresh waters where they spawn and may or may not die. For the studied population of Atlantic salmon, we found an annual mean net energy flux (ascending spawners – (descending smolts and kelts)) of 616×10^3 kJ from the ocean to the river. Sexual products and carcasses of dead spawners constituted about 70% of this. The rest (30%) is energy used during their river stay for maintenance, migration, reproductive activity, development of secondary sexual characters and defence. The surviving adults lost about 50% of their total energy during spawning in the River Imsa (Jonsson & Jonsson, submitted manuscript), and if we include the mortality of the spawners in the river, the energy loss because of reproduction was approximately 60%.

Such estimates of energy loss probably increase with the size of the fish and the costs of migration in the river (Jonsson *et al.*, 1997). In large rivers supporting multi-sea-winter salmon such as the River Drammen (mean flow 300 $m^3 s^{-1}$, mean length of the spawners 81 cm), the individual spawners lost between 60 and 70% of their total energy during reproduction, and the rate of mortality is also higher (Jonsson *et al.*, 1997). There, only 2% of the spawners returned from the sea as second time spawners. The corresponding figures for the River Imsa (mean flow 5.1 $m^3 s^{-1}$, mean length of the spawners 65 cm) were 40–50% energy loss and 8% repeat spawning (Jonsson *et al.*, 1991a, 1991b, 1997). In the River Drammen, the migratory distance is also longer (30 km) than in the River Imsa (1 km), so the migratory costs in the river should be higher. The salmon in the River Drammen stop feeding earlier in the season as they enter the river during summer, not in the autumn as in the River Imsa (Jonsson *et al.*, 1990).

Energy transfer varied considerably among years. The energy of the immigrating and emigrating salmon varied approximately 10 times the minimum population size (and for the gonadal products spawned much more), with coefficients of variance about 50%, and the variance in nutrient flux was even higher. This finding contrasts with that of Lyle & Elliott (1998), who reported that the coefficient of variation for the annual catch was only 8%, based on the angling records during 7 years of study. May be the rod catches vary less than the actual population abundance meaning that the catch efficiency decreased with increasing population density.

The reasons for the huge variations in immigration and emigration are probably large environmental fluctuations. The variation in smolt production is large even though juvenile survival is density dependent, with decreasing survival rate with increasing population size (Jonsson *et al.*, 1998a). The energy of the descending smolts also varies markedly, both due to different amounts of eggs spawned, number of fish present and probably also variability in factors such as temperature and flow. Survival at sea has been found to be density independent and variation in the number of returning adults is positively correlated with recruitment (Jonsson *et al.*, 1998a). However, sea survival also varies because of environmental fluctuations, and water temperature and ocean currents appear particularly important (Friedland *et al.*, 2000).

Except for Elliott *et al.* (1997) and Lyle & Elliott (1998), there are few studies estimating the nutrient export by anadromous salmonids in Europe from the sea to rivers. As wet mass, they found that the net flux to the River Tweed was approximately 60% of the gross import. In terms of energy, the corresponding figure for the River Imsa was 44%. The main reason for the difference is higher postspawning survival in the River Imsa than in the River Tweed. This difference may be because the River Tweed (mean flow 85 $m^3 s^{-1}$) is considerably larger than the River Imsa, resulting in large fish and higher postspawning mortality.

Adult Atlantic salmon enrich rivers with the constituents carbon, nitrogen and phosphorus as a consequence of their spawning and postspawning mortality. The quantities of these elements introduced by the fish may, however, appear small when compared with the mean export budgets of the river. For example, the typical mean weighed load of total phosphorus is 0.0048 g m^3 in the River Imsa, and based on measurements of NO_3-N, the approximate mean load of nitrogen has been estimated at 0.8 g m^3 for total nitrogen (Jonsson & Blakar, 1988; S. Lierhagen, Norwegian Institute for Nature Research, Trondheim, personal communication). The magnitude of annual export from the river is 130 t of total nitrogen and 0.770 t of total phosphorus per year, or a difference of 167% between the two elements. We have no estimate for carbon export. For the north-east English rivers, Lyle & Elliott (1998) found the river load for carbon to be 4.7 times higher than that for nitrogen.

Imported N and P via adults returning from the sea were in the order of 0.6% for nitrogen and 17% for phosphorus, and the export by smolts were much lower at 0.1 and 2.9%, respectively. The average net flux by adults, kelts and smolts was approximately 0.2% for nitrogen and 5% for phosphorus of the river loads. The contribution to the phosphorus load appears significant in some years, taking into account the large annual variation mentioned above. But other factors than salmonid fish are more important for the nutrient load in the River Imsa. The corresponding percentage in the north-east English rivers ranged between 0.09 and 0.24% which is considerably less than in the River Imsa. The difference becomes even more pronounced when we note that the English estimates included Atlantic salmon and brown trout whereas we have only studied salmon.

Migratory fish bring marine constituents into fresh waters and distribute otherwise unavailable, marine derivatives throughout river systems (Lyle & Elliott, 1998). Although not as important for the productivity in the Atlantic salmon rivers as in those supporting Pacific salmon on the west coast of North America (Larkin & Slaney, 1997; Cederholm *et al*., 1999; Helfield & Naiman, 2001), the effect may be important for the continued productivity of the river ecosystem. These percentages were higher than those recorded for rivers in north-east England, probably because the nutrient loads were generally higher in the latter rivers compared with Norwegian west coast rivers; twice as high for nitrogen and more than 50 times higher for phosphorus. Thus, even though the nutrient flux was smaller in the River Imsa, its effect still appears significant for a river relatively poor in nutrients.

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References

Ben-David M., Hanley T.A. & Schnell D.M. (1998) Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos*, **83**, 47–55.

Bilby R.E., Fransen B.R. & Bisson P.A. (1996) Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 164–173.

Bilby R.E., Fransen B.R., Bisson P.A. & Walter J.K. (1998) Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in south-western Washington, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1909–1918.

Carlin B. (1955) Tagging of salmon smolts in the river Lagan. *Report of the Institute of Freshwater Research Drottningholm*, **36**, 57–74.

Cederholm J.C., Kunze M.D., Murota T. & Sibatani A. (1999) Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries*, **24**, 6–15.

Chaloner D.T., Wipfli M.S. & Caouette J.P. (2002) Mass loss and macroinvertebrate colonisation of Pacific salmon carcasses in south-eastern Alaskan streams. *Freshwater Biology*, **47**, 263–274.

Elliott J.M., Lyle A.A. & Campbell R.B.N. (1997) A preliminary evaluation of migratory salmonids as vectors of organic carbon between marine and freshwater environments. *Science of the Total Environment*, **194**, 219–223.

Friedland K.D., Hansen L.P., Dunkley D.A. & MacLean J.C. (2000) Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine Science*, **57**, 419–429.

Garman G.C. & Macko S.A. (1998) Contribution of marine-derived organic matter to an Atlantic coast, freshwater, tidal stream by anadromous clupeid fishes. *Journal of the North American Benthological Society*, **17**, 277–285.

Gresh T., Lichatowich J. & Schoonmaker P. (2000) An estimation of historical and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries*, **25**, 15–21.

Helfield J.M. & Naiman R.J. (2001) Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology*, **82**, 2403–2409.

Jonsson B., Jonsson N. & Hansen L.P. (1991a) Differences in life history and migratory behaviour between wild and hatchery reared Atlantic salmon in nature. *Aquaculture*, **98**, 69–78.

Jonsson N. & Blakar I.A. (1988) Kjemisk overvåkning av norske vassdrag 1987. *Direktoratet for Naturforvaltning, Rapport Fra Fiskeforskningen*, **3**, 1–72. (In Norwegian)

Jonsson N., Hansen L.P. & Jonsson B. (1991b) Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. *Journal of Animal Ecology*, **60**, 937–947.

Jonsson N., Jonsson B. & Hansen L.P. (1990) Partial segregation in the timing of migration of Atlantic salmon of different ages. *Animal Behaviour*, **40**, 313–321.

Jonsson N., Jonsson B. & Hansen L.P. (1997) Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, **66**, 425–436.

Jonsson N., Jonsson B. & Hansen L.P. (1998a) Density-dependent and density-independent relationships in the life cycle of Atlantic salmon, *Salmo salar*. *Journal of Animal Ecology*, **67**, 751–762.

Jonsson N., Jonsson B. & Hansen L.P. (1998b) Long-term study of the ecology of wild Atlantic salmon smolts in a small Norwegian river. *Journal of Fish Biology*, **52**, 638–650.

Jonsson N., Jonsson B. & Ruud-Hansen J. (1988) Downstream displacement and life history traits of whitefish, *Coregonus lavaretus*, in a Norwegian river. *Environmental Biology of Fishes*, **23**, 197–204.

Kline T.C., Goering J.J., Mathisen O.A., Poe P.H. & Parker P.L. (1990) Recycling of elements transported upstream by runs of Pacific salmon: I. δ^{15}N and δ^{13}C evidence in Sashin Creek, southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 136–144.

Kline T.C., Goering J.J., Mathisen O.A., Poe P.H., Parker P.L. & Scalan R.S. (1993) Recycling of elements transported upstream by runs of Pacific salmon. I. δ^{15}N and δ^{13}C evidence in Kvichak River watershed, Bristol Bay, southwestern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2350–2365.

Kline T.C., Goering J.J. & Piorkowski R.J. (1997) The effect of salmon carcasses on Alaskan freshwaters. In: *Freshwater of Alaska: Ecological Syntheses* (Eds A.M. Milner & M.W. Oswood), pp. 179–204. Springer-Verlag, New York.

Larkin G.A. & Slaney P.A. (1997) Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. *Fisheries*, **22**, 16–24.

Lyle A.A. & Elliott J.M. (1998) Migratory salmonids as vectors of carbon, nitrogen and phosphorus between marine and freshwater environments in north-east England. *Science of the Total Environment*, **210**/211, 457–468.

Michael J.H. (1998) Pacific salmon spawning escapement goals for the Skagit River watershed as determined by nutrient cycling considerations. *Northwest Science*, **72**, 239–248.

Mills D.H. (1986) The biology of Scottish salmon. In: *The Status of Atlantic Salmon in Scotland* (Ed. W.M. Shearer), pp. 10–19. Institute of Terrestrial Ecology, Abbots, Ripton, UK.

Minakawa N. & Gara R.I. (1999) Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning run in a small stream of the Pacific Northwest. *Journal of Freshwater Ecology*, **14**, 327–335.

Ricker W.E. (1979) Growth rates and models. In: *Fish Physiology*, Vol. 8 (Eds W.S. Hoar, D.J. Randall & J.R. Brett), pp. 677–743. Academic Press, New York.

Talbot C., Preston T. & East B.W. (1986) Body composition of Atlantic salmon (*Salmo salar* L.) studied by neutron activation analysis. *Comparative Biochemistry and Physiolohy*, **85A**, 445–450.

Wipfli M.S., Hudson J. & Caouette J. (1998) Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1503–1511.

Wipfli M.S., Hudson J.P., Chaloner D.T. & Caouette J.P. (1999) Influence of salmon spawner densities on stream productivity in Southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1600–1611.

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